Pre-stimulus alpha oscillations over somatosensory cortex predict tactile misperceptions

Abbreviated title: Pre-stimulus α and peri-threshold touch

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Abstract

Fluctuations of pre-stimulus oscillatory activity in the somatosensory alpha band (8-14 Hz) observed using human EEG and MEG have been shown to influence the detection of supra- and peri-threshold somatosensory stimuli. However, some reports of touch occur even without a stimulus. We investigated the possibility that pre-stimulus alpha oscillations might also influence these false reports of touch – known as tactile misperceptions. We recorded EEG while participants performed the Somatic Signal Detection Task (SSDT), in which participants must detect brief, peri-threshold somatosensory targets. We found that pre-stimulus oscillatory power in the somatosensory alpha range exhibited a negative linear relationship with reporting of touch at electrode clusters over both contralateral and ipsilateral somatosensory regions. As pre-stimulus alpha power increased, the probability of reporting a touch declined; as it decreased, the probability of reporting a touch increased. This relationship was stronger on trials without a somatosensory stimulus than on trials with a somatosensory stimulus, although was present for both trial types. Spatio-temporal cluster-based permutation analysis also found that pre-stimulus alpha was lower on trials when touch was reported – irrespective of whether it was present – over contralateral and ipsilateral somatosensory cortices, as well as left frontocentral areas. We argue that alpha power may reflect changes in response criterion rather than sensitivity alone. Low alpha power relates to a low barrier to reporting a touch even when one is not present, while high alpha power is linked to less frequent reporting of touch overall.

Keywords: EEG; pre-stimulus; alpha oscillations; somatosensory; perception; signal detection

Introduction

Fluctuations of oscillatory activity in the somatosensory alpha range (8-14 Hz) observed using the human EEG and MEG have been shown to influence detection of supra-, peri-, and sub-threshold somatosensory targets. Specifically, detection of targets improves and declines according to the power and phase of ongoing alpha oscillations over (typically) contralateral primary somatosensory cortex (Ai & Ro, 2014; Jones et al., 2010; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004; Weisz et al., 2014; Zhang & Ding, 2010). Alpha has been linked to cortical excitability, which may be the underlying mechanism that links observed alpha with performance (e.g. Rajagovindan & Ding, 2010; Romei, Brodbeck, et al., 2008; Romei, Rihs, Brodbeck, & Thut, 2008). However, the influence of oscillatory power on the false alarm rate – reports of stimuli which are not there – has often been neglected. In vision, some reports have suggested that alpha power may determine responses to absent stimuli (Limbach & Corballis, 2016) or misperceptions of one stimulus as two (Lange, Oostenveld, & Fries, 2013). Understanding how ongoing activity relates to both hits and false alarms may be critical to understanding the functional role of alpha oscillations in tactile perception.

Alpha power has been strongly linked to cortical excitability and inhibition (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007; Romei, Brodbeck, et al., 2008), with low alpha power indicating that a region is in a state of high excitability, and high alpha power indicating low excitability or inhibition. Trial-to-trial fluctuations in power might account for variations in the detectability of stimuli: A weak stimulus might be sufficient to produce a response from a region in a low-alpha, high-excitability state, but insufficient when that region is in a high-alpha, low-excitability state. Alpha oscillations may thus reflect pulses of cortical inhibition (Mathewson et al., 2011), as a sensory region adjusts to temporal expectations of the delivery of a stimulus by ensuring it is in high-excitability state when a

stimulus is expected. Top-down manipulation of alpha power may also be a mechanism for the suppression of irrelevant stimuli (Haegens, Händel, & Jensen, 2011), through the inhibition of cortical regions dealing with, for example, unattended regions of space. This may also be used to gate communication between different cortical regions (Jensen, Bonnefond, & VanRullen, 2012; Jensen & Mazaheri, 2010), allowing or preventing early sensory responses to reach consciousness (Weisz et al., 2014).

Although alpha has most frequently been shown to have a negative linear relationship with detection of visual targets, with lower alpha power increasing hit-rates (Busch, Dubois, & VanRullen, 2009; Ergenoglu et al., 2004; Hanslmayr et al., 2007), the pattern of the relationship between somatosensory alpha and performance is much more mixed. Several groups have reported a similar negative linear relationship between alpha and performance as that seen in vision, with low alpha power associated with better performance on both tactile detection tasks and simultaneity judgement tasks (Baumgarten, Schnitzler, & Lange, 2016; Jones et al., 2010; van Ede, Köster, & Maris, 2012). This suggests that pre-stimulus somatosensory and visual alpha may share common functional roles and mechanisms. However, several other groups have reported a quadratic relationship between alpha and performance, with intermediate power levels associated with improved hit rates (Ai & Ro, 2014; Linkenkaer-Hansen et al., 2004; Weisz et al., 2014; Zhang & Ding, 2010).

Notably, the role of pre-stimulus alpha in false reports of a tactile or visual stimulus was not directly addressed in any of these studies. High cortical excitability may also be expected to increase false alarms if the state of the system is such that even a weak stimulus is sufficient to generate a large response. Participants may be more likely to erroneously respond to non-target stimuli or endogenously generated sensations as well as genuine stimuli. Consistent with this suggestion, a recent report suggests that alpha power during visual tasks may modify response criterion rather than visual sensitivity (Limbach &

Corballis, 2016). They found that participants were more likely to report a stimulus when alpha was low than when alpha was high. Both hit rates and false alarms decreased as alpha power increased, suggesting a tightening of response criterion but no increase in sensitivity with increasing power. Similarly, Samaha, Iemi and Postle (2016) reported that alpha power negatively correlated with participants' confidence in their responses in a visual two-choice orientation discrimination task, but did not predict the accuracy of those responses. Sherman, Kanai, Seth, and VanRullen (2016) also report that alpha phase, which may index moment-by-moment excitability, determined response criterion in a visual detection task. Participants' reports of the presence or absence of a stimulus were partially predicted by phase at stimulus onset, regardless of whether their decision was correct.

Although there is evidence suggesting that alpha oscillations may shift response criterion or confidence in visual tasks, evidence for shifting the response criterion in touch is, in contrast, lacking. In macaques, Haegens et al. (2014) reported that alpha oscillations in contralateral primary somatosensory cortex shifted response criterion rather than tactile sensitivity. Higher alpha power was associated with a lower criterion, and thus an increase in stimulus-present responses regardless of whether the stimulus was present. Notably, this is the opposite pattern to that reported by Limbach and Corballis (2016) in humans in vision, suggesting that somatosensory related alpha power may function in a different way than in alpha power visual tasks.

We examined alpha oscillations using electroencephalography (EEG) recorded while participants performed the Somatic Signal Detection Task (SSDT; Lloyd, Mason, Brown, & Poliakoff, 2008). In the SSDT, participants detect brief somatosensory stimuli delivered to their non-dominant hand at their individual perceptual threshold. In addition, an LED placed close to the non-dominant hand flashes during the SSDT, sometimes simultaneous with the tactile stimulus and sometimes on its own. The presence of the LED has previously been

shown to increase false alarm rates (Brown, Brunt, Poliakoff, & Lloyd, 2010; Lloyd et al., 2008; Lloyd, McKenzie, Brown, & Poliakoff, 2011). A common impediment to examining the relationship between alpha power and false alarms is the relative lack of false alarm trials to examine. False alarm rates in many tasks are typically below 15% (e.g. Busch et al., 2009; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). The SSDT typically yields false alarm rates of 15-20 %. Thus, the SSDT offers an excellent paradigm for examining somatosensory performance and specifically for producing sufficient false alarms to quantitatively investigate how alpha oscillations relate to both true and false reports of touch.

Materials and Methods

Participants

In total, we recruited 32 right-handed participants (age range = 18 to 45 years, mean age = 22 years, S.D. = 6 years, 28 female) drawn from the participant pool at the University of Leeds. Participants provided written, informed consent to take part and the experimental procedure was approved by the Ethical Committee of the School of Psychology at the University of Leeds. All participants had normal or corrected-to-normal vision and reported no tactile deficits.

Apparatus

The stimulus array comprised a rectangular block in which a piezoelectric tactile stimulator (PTS) was embedded (Dancer Design, St. Helens, UK), with a rectangular 6 mm × 4 mm red light-emitting diode (LED) attached to the block, adjacent to the PTS. The participants' left index finger was placed on top of the PTS and held in position using a double-sided adhesive pad. The array was placed to the left of the participants' midline. Note that the casing of the PTS was rigid plastic and minimized extraneous vibration beyond the point of stimulation,

attenuating noise generated by the PTS. Coupled with background ambient noise from the experimental PC, this prevented the PTS from being audible at the stimulation levels used throughout the experiment. No participants reported that the PTS was audible. Participants responded with a cylindrical button box held in their right hand. Tactile stimuli were produced using amplified sound waves from a PC. A monitor located behind the stimulus array delivered instructions and visual cues. Participants sat in a light-attenuated room approximately 70cm in front of the monitor.

Design and procedure

Thresholding procedure. Participants performed two distinct experimental phases. They first performed a block of tactile thresholding trials, which followed a Parameter Estimation by Sequential Testing (PEST; Taylor & Creelman, 1967) staircase procedure. Each trial consisted of two 1020 ms time periods. Each time period began with a green arrow presented for 500 ms on the left side of the monitor and pointing down towards the participant's finger. The number one ('1') was superimposed on the first arrow, while the number two ('2') was superimposed on the second arrow. A 20 ms tactile pulse was delivered in one of these periods, 500 ms after the offset of the respective arrow, and was followed by a blank screen for a further 500 ms. When no stimulus was presented, the screen remained blank after the cue offset for 1020 ms. After both time periods had elapsed, participants were prompted on screen to press button 1 or 2 on the button box to report whether the stimulus had been presented in the first or second time period respectively.

The intensity of the tactile pulse was defined on a scale of arbitrary units ranging from a maximum intensity of 0 to a minimum intensity of -10000. A Wald sequential probability ratio test (SPRT) was used to determine when to change the strength of the tactile pulse. Specifically, the SPRT was conducted by calculating the W statistic after each trial as (N(c) -

Pt.) × N(t), where N(c) = number of correct responses since last step change, Pt = desired probability threshold (in this case, 75%), and N(t) = number of trials completed since last step change. When participants' correct responses were significantly greater than 75%, this caused the Wald SRPT to be greater than W = 1, and a weaker vibration level was selected (step-down). When participants' correct responses were significantly less than 75% this caused the Wald SRPT to be less than W= -1, and a stronger vibration level was selected (a reversal). The initial step size was 800. Minimum step size was set at 50. Maximum step size was set at 3200. A maximum of 250 trials were completed in this phase, with breaks allowed after 100 and 200 trials.

Experimental phase. After completing thresholding, participants began the main experimental phase: the Somatic Signal Detection Task (SSDT). Each experimental trial began with a green arrow on the left side of the screen for 750 ms. After a randomly varying post-cue period of from 2250 ms to 1500 ms, a 20 ms event period occurred. Participants received either a 20 ms tactile pulse at the threshold determined in the first phase, a 20 ms light flash, a combined 20 ms tactile pulse and simultaneous light flash, or no stimulus. Following a delay of 750 ms after the stimulus event period, a response screen appeared. Participants were given four response options: "definitely yes", "maybe yes", "maybe no", "definitely no". They responded using a button box held in their right hand. Participants were explicitly told to ignore the light and to respond when they felt a touch irrespective of whether a light was presented or not. There were 102 trials of each type: touch only, light only, both light and touch, or no stimulus. There were 408 trials in total, split into six blocks of 68 trials to allow participants brief rest periods during the EEG recording. There were 17 trials of each trial type within each recording block.

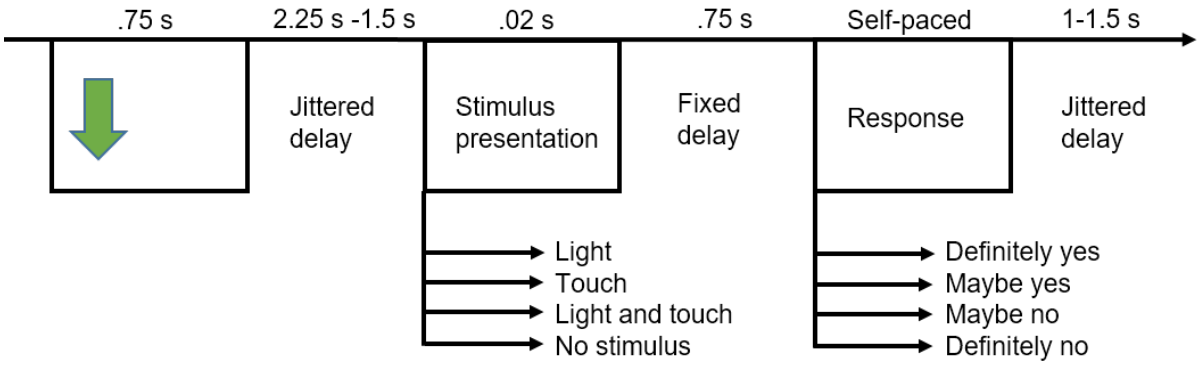

Figure 1 Trial outlook for the Somatic Signal Detection Task. Trials began with a visual cue, followed by a blank screen until the stimulus event period. One of four possible event types occurred, followed by a fixed delay of .75 s until the onset of the response screen.

EEG recording and processing

EEG was recorded continuously from 62 scalp locations at a sampling rate of 1000 Hz using a Neuroscan Quik-Cap attached to a SynAmps2 amplifier (Compumedics, Charlotte, NC, USA). Four electrooculograms (EOG) – above and below the left eye, and at the outer canthi of each eye – were recorded in order to exclude trials with excessive eye movements. Two additional electrodes were placed at left and right mastoids. The recording was referenced online to an electrode placed between electrodes Cz and CPz, while an electrode positioned at Fz served as ground. EEG processing was performed using the EEGLAB (Delorme & Makeig, 2004) and Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) toolboxes combined with in-house procedures running under the Matlab (The Mathworks, Inc., Natick, Massachusets) environment. The data were re-referenced offline to the average of all channels. Continuous data were filtered with a high-pass FIR filter with a cut-off at 0.5 Hz (passband = 1 Hz, order = 1650). The EEG data were segmented into epochs beginning 2250 ms before and lasting 1250 ms after the potential onset of a stimulus. After epoching, the Fully Automated Statistical Thresholding for EEG Artefact Rejection plugin for EEGLAB

(Nolan, Whelan, & Reilly, 2010) was used for general artefact rejection and interpolation of globally and locally artefact contaminated channels, supplemented by visual inspection for further periods of non-standard data, such as voltage jumps, blinks, and muscle noise.

We estimated oscillatory power in the range from 4 to 30 Hz in 1 Hz steps using a single Hann taper with an adaptive time window equal to four cycles at each frequency. With single Hann tapers, the degree of frequency smoothing is equivalent to ± 1/window length. Power was estimated at 20 ms intervals from 2 seconds before stimulus onset until 1 second after stimulus onset. For our regression-based single-trial and cluster-based analyses of power, we extracted estimates of power at 11 Hz, where the window length was 364 ms. This yielded a frequency smoothing of ± 1000/364 ms, or ± 2.75 Hz. Thus, we smoothed our estimates over a band of power from 8.25-13.75 Hz, encompassing the typical range of individual alpha frequencies. We retained power estimates for all trials from all conditions.

Behavioural data

We analysed the proportion of trials on which touches were reported using a two-way repeated measures ANOVA with the factors touch (present/absent) and light (present/absent). Generalized eta squared (η^2_g.) was reported as a measure of effect size. In addition, we calculated sensitivity (d′) and criterion (*c*) for the light-present and light-absent trials, using the log-linear correction to correct for 0% and 100% hit or false alarm rates, and compared those using two-tailed paired t-tests. All statistics were performed using R 3.3.1 (R Core Team, 2015). Significant interactions were followed up using post-hoc t-tests with Bonferroni-Holm correction for multiple comparisons.

Single-trial analysis of somatosensory alpha power

Alpha power estimates were obtained by averaging power at 11 Hz (± 2.75 Hz) from -600 ms to -200 ms before stimulus onset across clusters of electrodes over right and left centro-parietal regions (i.e., right: C2, C4, CP2, CP4; left: C1, C3, CP1, CP3). Note that the taper length of 364 ms at 11 Hz means that average estimates from -600 ms to -200 ms before stimulus onset integrates data from timepoints from -782 ms until -18 ms before stimulus onset, and thus avoids smearing of post-stimulus activity into the pre-stimulus period. Somatosensory alpha effects in similar experiments involving detection of tactile stimuli have been found at comparable locations on the right hemisphere; while the left hemisphere electrodes are the direct homologue of those locations (Ai & Ro, 2014; Schubert, Haufe, Blankenburg, Villringer, & Curio, 2008; Zhang & Ding, 2010). The response on each trial was coded as "reported-yes" if the participants responded "definitely yes" or "maybe yes", or "reported-no" if the participant responded "definitely no" or "maybe no". The primary purpose of the "maybe" options was to encourage false alarms (Brown et al., 2010; Lloyd et al., 2008), and thus we chose to collapse across these options for analytical simplicity.

We modelled the relationship between single trial alpha power and behavioural response using a generalized linear mixed-effects model (GLMMs) with a logistic link function. GLMMs are an extension of generalized linear models (e.g., logistic regression) that allow for the inclusion of both random and fixed effects. Standard logistic regression assumes independence of observations and is thus unsuitable for the analysis of a repeated-measures design. GLMMs can incorporate the dependence structure of the observations into the model using random effects.

We used the *mixed* function from the *afex* package (Singmann, Bolker, Westfall, & Aust, 2016) for R (R Core Team, 2015) to fit our GLMMs and perform likelihood ratio tests to establish the significance of all main effects and interactions. The *afex* package uses the *glmer* function from the *lme4* package for model fitting (Bates, Mächler, Bolker, & Walker,

2015, 2016). In keeping with Barr, Levy, Scheppers, and Tily (2013), we fit the maximal model to our data. Specifically, the model was specified by the following syntax in R:

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reported ~ Touch * Light * Alpha + (1 + Touch * Light * Alpha | Participant)
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This specification indicates that the response variable on the left side of the ~ operator should be modelled as a function of the terms on the right side of the ~ operator. Terms outside of the brackets specify fixed effects, while terms inside the brackets specify random effects and slopes. The * operator indicates that main effects and interactions should be included in the model. Thus, the fixed effects were the single-trial estimates of somatosensory alpha, the presence of touch (present/absent), the presence of light (present/absent), and all interactions between these factors. Participant was specified as a random effect, random slopes were estimated for all main effects and interactions, and the correlations between these slopes and the random intercept were also estimated. Contrasts were sum-coded. We coded the outcome of each trial as a 1 or a 0 based on the participants' response (1: reported "definitely" or "maybe" yes; 0: reported "definitely" or maybe "no").

The estimates of alpha power were mean-centred and scaled to one standard deviation within each participant, allowing the GLMM to estimate within-subject effects efficiently and without conflation with between-subject variability. Likelihood ratio tests compare the goodness-of-fit of two models, and are performed by systematically removing each fixed effect term from the full model and comparing the log-likelihood of the model with the term to the log-likelihood of the model without the term. This provides a chi-square statistic and a *p*-value which indicate whether the term significantly improves the model. Where individual coefficients were tested in follow-up tests of interactions, reported *p*-values and chi-square statistics are based on likelihood ratio tests of the model with the fixed effect of interest against the model without the fixed effect of interest.

Analysis of binned alpha power

The majority of previous examinations of the relationship between alpha and performance have followed the following procedure: 1) trials are binned in order of increasing spectral power, typically using either a quartile or decile split 2) a mean hit rate, a "normalized detection rate", or signal detection measure is calculated for each bin 3) binned power is entered as a factor in a repeated measures ANOVA, with hit rate as the dependent variable (for examples of such approaches, see Busch et al., 2009; Jones et al., 2010; Limbach & Corballis, 2016; Linkenkaer-Hansen et al., 2004; Zhang & Ding, 2010). However, dichotomizing continuous variables typically reduces statistical power, and obscures the relationship between the variable and the outcome measure. This can be particularly problematic when the continuous variable in question is not normally distributed; spectral power in any frequency range typically has a strongly positive skewed distribution that is approximately log-normal.

Thus, to compare the results of our GLMM analysis with previous findings, and to elucidate some of the issues with the typical binning procedures, we also analysed performance as a function of binned alpha power. We binned alpha power for each participant into quartiles and deciles, separately for each hemisphere. Note that there is no clear rationale to determine how many bins are necessary. Too few bins may fail to capture local features of the underlying distribution; too many may instead be overly influenced by local variation in the underlying distribution. After binning, we calculated the mean reporting rate for each participant for each bin, for each hemisphere and performed separate repeated measures ANOVAs for the quartile and decile binned data with the factors Touch (present/absent), Light (present/absent and Bin (quartile or decile) with mean reporting rate as the dependent variable. We also performed these analyses separately on each hemisphere

rather than include it as a factor. In order to include hemisphere as a factor, we would need to combine alpha across both hemispheres before ranking all trials. This would lead to varying numbers of cells in the design across each condition, and possibly empty cells. For example, a participant may have few or no trials where alpha power in the left hemisphere was in the 4^{th} quartile and both tactile and light stimuli were delivered.

To investigate the underlying relationship between mean alpha power for each bin we also performed linear, quadratic, and cubic contrasts of mean alpha power. Note that alpha power was not baseline corrected for this part of the analysis. Greenhouse-Geisser correction was applied in order to correct violations of sphericity; where this was done, corrected degrees of freedom are reported. ANOVAs were performed using the *afex* package (Singmann et al., 2016), with follow-up contrasts performed using *lsmeans* (Lenth, 2016).

Exploratory cluster-based analysis of somatosensory alpha

We also examined power in the alpha band across all sensors and all time-points from -1s to 0s (potential stimulus onset time) using cluster-based non-parametric permutation tests as implemented in the Fieldtrip toolbox (Maris & Oostenveld, 2007). We used a cluster-forming threshold of $p = .05$ and allowed clusters to be formed across space and time, with 2 electrodes specified as the minimum number of electrodes to be considered as a neighbouring spatial cluster. The sum of the t-values within each cluster of significant datapoints was used as a cluster-level statistic. The threshold for significance at a FWE-corrected alpha of $p = .05$ was established using 2500 random permutations of the data to construct a null distribution. For each permutation, each data point was randomly allocated to a condition and clusters formed as above. The sum of the t-values of the maximum size cluster for each permutation was then taken as the test statistic, forming a reference distribution of maximum cluster t values under the null hypothesis of no difference between conditions. Values below or above

the 2.5th and 97.5th percentile of this distribution were considered significant. For this analysis, we compared alpha power on trials where a touch was reported to activity on trials where no touch was reported, irrespective of whether a touch was present.

Results

Behavioural data

Participants reported far more touches when touch was present than when it was absent [$F(1,31) = 66.9$, $p < .001$, $\eta^2_g = .53$], and more touches when light was present than when it was not [$F(1,31) = 35.69$, $p < .001$, $\eta^2_g = .11$]. In addition, there was a significant interaction between light and touch [$F(1,31) = 18.51$, $p < .001$, $\eta^2_g = .02$], (see Figure 2). Post-hoc tests indicated that all means were significantly different from each other (all $p < .002$). The interaction was driven by the noticeably larger effect of the light on touch trials. Thus, touch and light combined increased hit rate more than it increased false alarm rate. Indeed, participants exhibited significantly higher sensitivity ($t(31) = 2.66$, $p = .01$) on trials when a light was presented ($d' = 1.25$) than on trials without a light ($d' = 1.06$). There was no significant difference in criterion ($t(31) = -1.72$, $p = .09$), despite a numerically less stringent criterion on trials with a light ($c = .59$) compared to trials with no light ($c = 1.18$).

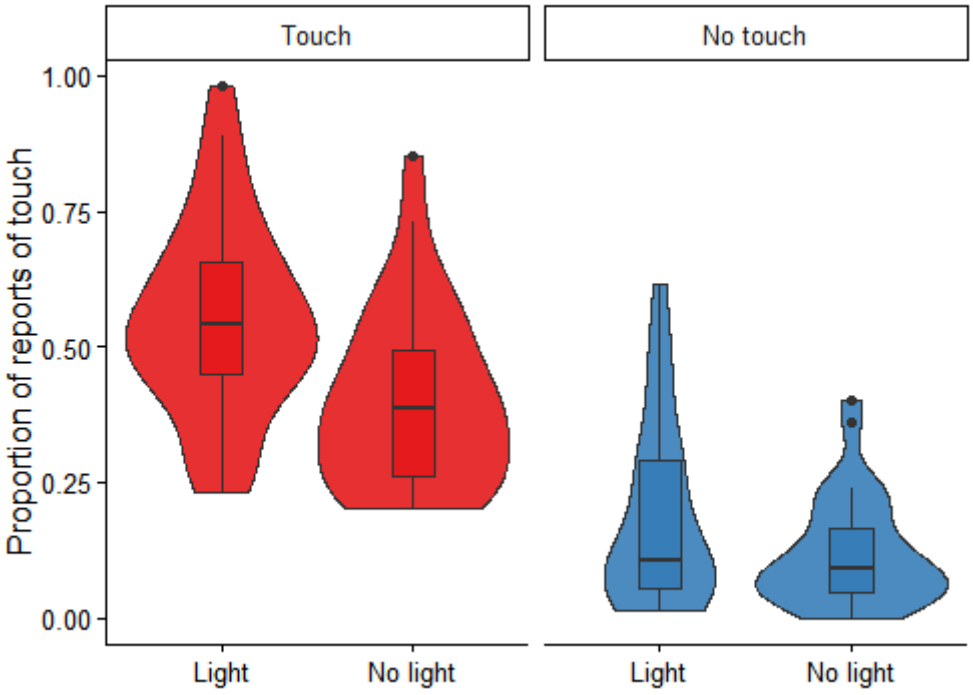

Figure 2 Violin plots of the proportion of reports of touch for each trial type. Red indicates trials with a touch, blue indicates trials with no touch. The width of the violin is determined by a kernel density estimate of the distribution of individual response proportions (i.e., a wider violin indicates more participants responding within a given range). Overlaid boxplots show the median of the distribution, indicated by the black line, and the 25% and 75% quartiles using the lower and upper hinges of the box respectively. Outliers - defined as values more than 1.5 times the interquartile range below or above the 25% and 75% quartiles - are indicated by black dots.

EEG

Figure 3 shows time-frequency plots of a) spectral power across each of the four trial types and b) theratio of spectral power on reported-yes to reported-no trials from 4 - 30 Hz. As expected, a clear band of activity is visible centred at approximately 11 Hz spanning the

entire time window at both ipsilateral left (C1, C3, Cp1, and Cp3) and contralateral right (C2, C4, Cp2, Cp4) electrode clusters. Notably, the ratio between the reported-yes and reported-no trials indicates lower power in this frequency band before the potential stimulus onset (marked by the dashed vertical lines), with clear post stimulus differences also visible.

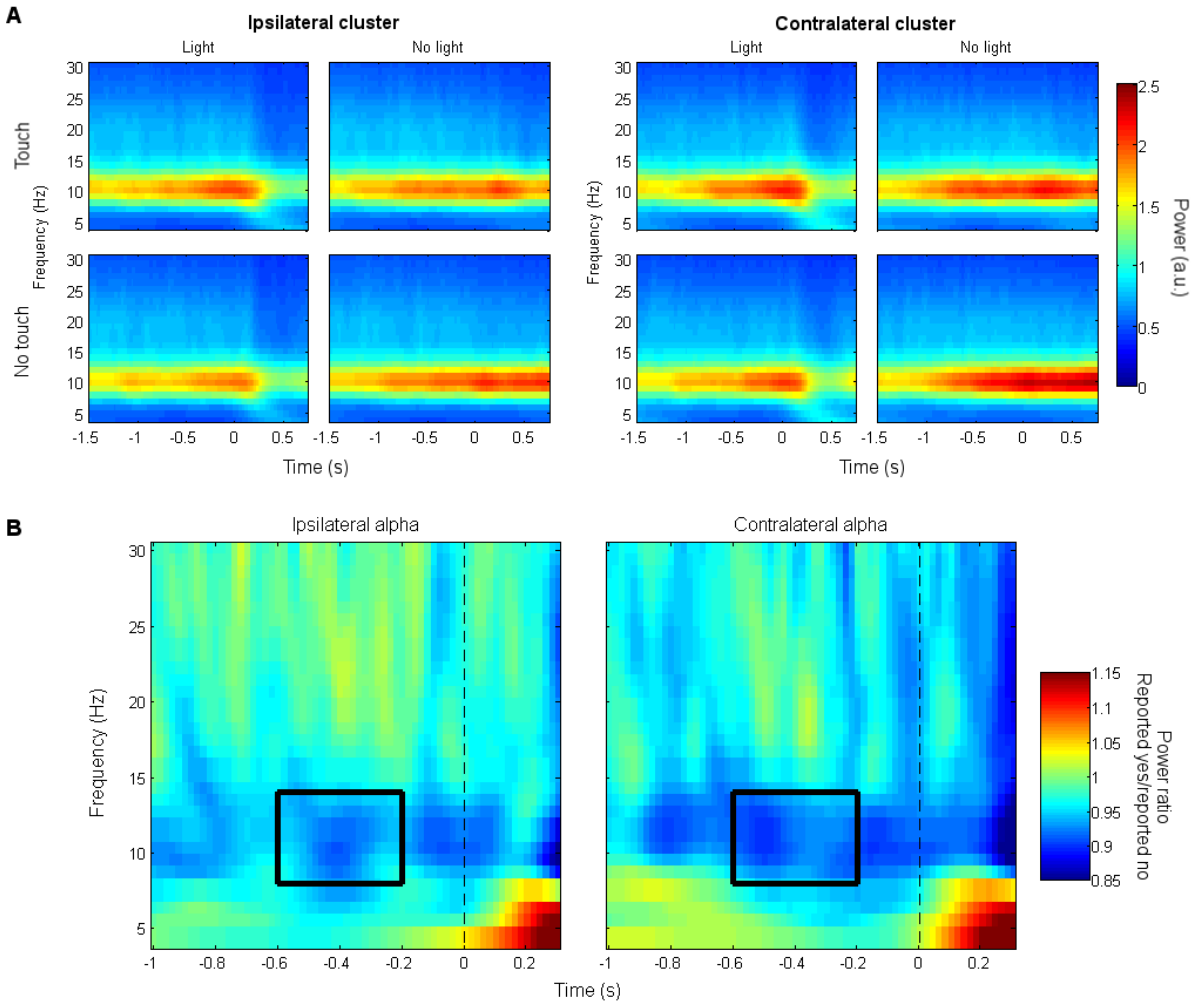

Figure 3. Grand mean time-frequency plots of A) (uncorrected) spectral power from 4-30 Hz for each trial type and B) the difference in spectral power from 4-30 Hz at the ipsilateral left and contralateral right centro-parietal clusters of interest. Plots in B show the ratio of spectral power on reported-yes trials to spectral power on reported-no trials. Red means power was higher on reported-yes trials, blue means power was higher on reported-no trials. The vertical dashed lines indicate the

potential stimulus onset time. The black rectangle indicates the period used in the single-trial regression analysis.

Figure 4 shows mean alpha power (8-14 Hz) averaged from -.6 s to -.2 s before stimulus onset in the reported-yes and reported-no conditions, and the ratio of the difference between them. Notably, clear peaks of posterior alpha power are visible, with greater power on sensors contralateral to the tactile and visual stimulus, which were presented to the left hand. The difference plot suggests that power is typically lower across many electrodes on reported-yes trials versus reported-no trials, with the greatest difference over contralateral centro-parietal and parieto-occipital electrodes. We fitted generalized linear mixed effects models as specified above to the ipsilateral and contralateral centro-parietal regions of interest indicated on Figure 4B.

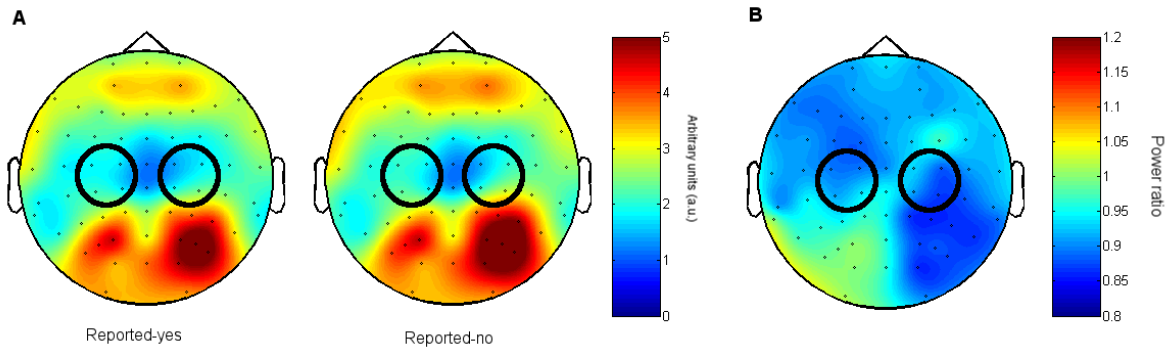

Figure 4. Alpha power for reported-yes and reported-no conditions. A) Grand mean alpha power (8-14 Hz) for the reported-yes and reported-no conditions, averaged over all subjects and from -.6 s to -.2s before the potential stimulus event. B) Ratio of spectral power between the reported-yes and reported-no conditions. Red indicates higher power on reported-yes trials, blue higher power for the reported-no trials. Black circles indicate the a priori regions of interest, left and right centro-parietal electrodes over ipsi- and contra-lateral primary somatosensory cortex.

Contralateral alpha

For the contralateral cluster of electrodes, alpha power was a significant predictor of performance overall (main effects of the presence of touch and the presence of light were also significant but will not be considered further, see Table 1 and Figure 5). Notably, there was also a significant interaction between alpha and touch. We examined this interaction by fitting reduced models containing only the fixed effect of alpha power, the random effect of subject, and a random slope for alpha power to the touch present and touch absent trials separately. For touch trials, the estimated coefficient of alpha was -.10 (±.04 SE; $\chi^2 = 5.93$, $p = .01$), equivalent to an odds ratio of 0.91. For no touch trials, the estimated coefficient of alpha was -.28 (±.08 SE; $\chi^2 = 17.86$, $p < .001$), an odds ratio of 0.76. Thus, on all trials increases in alpha power indicated a lower probability of reporting a touch. However, alpha was a stronger influence on reporting of touch on touch-absent than touch-present trials (see Figure 5).

Effect	χ^2	*p*	Coefficient (±SE)	Odds ratio (95% CI)
Contralateral alpha power	18.94	<.0001	-.20 (.05)	0.82 (0.74 – 0.90)
Touch	34.3	<.0001	1.07 (.13)	2.92 (2.23 – 3.80)
Light	11.94	.0005	.23 (.06)	1.26 (1.13 – 1.42)
Alpha:Touch	6.40	.01	.11 (.05)	1.11 (1.02 – 1.22)
Alpha:Light	.52	.5	-.03 (.04)	0.97 (0.89 – 1.06)
Touch:Light	8.15	.004	.10 (.04)	1.11 (1.03 – 1.19)
Alpha:Touch:Light	.19	.66	.02 (.04)	1.02 (0.94 – 1.11)
Intercept			-1.12(.12)	0.33 (0.26 – 0.41)

Table 1. Summary of the fixed effects of GLMMs of contralateral alpha and its influence on reporting of touch. χ^2 statistics derived from likelihood ratio tests, with associated *p*-values. Coefficients and odds ratios reported are from the maximal model as defined above. 95% confidence intervals were calculated using Wald statistics.

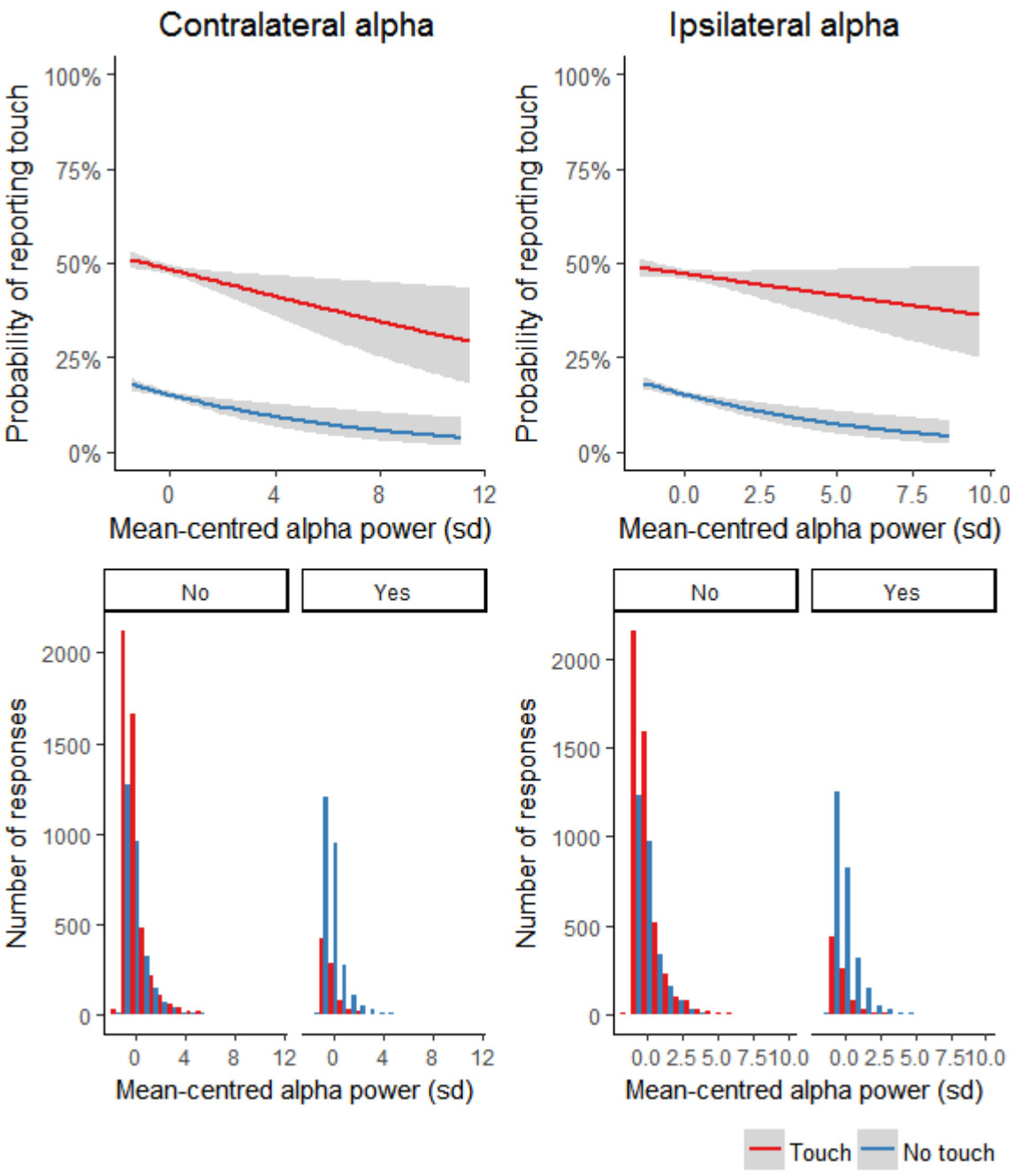

Figure 5. Predicted relationship between mean-centred alpha power and the probability of reporting a touch, and distributions of yes and no responses. Upper

row: Lines indicate the estimated relationship between alpha power and reporting that a touch is present. The red line indicates the relationship on touch-present trials (i.e., hit rate). The blue line indicates the relationship on touch-absent trials (i.e., false alarm rate). Shaded grey areas indicate 95% confidence intervals around the predictions. Lower row: histograms showing the overall frequency of a yes and no responses at bins centred every 0.75 standard deviations from the minimum mean-centred alpha power. Red bars = responses on touch trials. Blue bars = responses on no-touch trials.

Ispilateral alpha

For our ipsilateral region of interest, alpha was a significant predictor of reported touch overall and, again, there was a significant interaction between alpha and touch indicating that the slope of the relationship between touch and alpha was less negative when a touch was present (see Table 2 and Figure 5). For touch-present trials, alpha power was no longer a significant predictor of reporting of touch (coefficient: -0.05, SE = ±0.03, odds ratio: 0.95; χ^2 = 3.38, p = .07), despite a trend in the same direction. For touch-absent trials, alpha was still a significant predictor of reporting of touch (coefficient: -0.27, SE = ±0.08, odds ratio: 0.76; χ^2 = 17.95, p < .001). Relatively low ipsilateral alpha was thus associated with an increase in false alarm rate, while relatively high ipsilateral alpha was associated with a decrease in false alarm rate.

Effect	χ^2	p	Coefficient (±SE)	Odds ratio (95% CI)
Ipsilateral alpha power	20.05	<.0001	-0.17 (0.04)	0.84 (0.78 – 0.92)
Touch	34.5	<.0001	1.06 (0.14)	2.89 (2.22 – 3.78)

Light	14.03	.0002	0.25 (0.06)	1.28 (1.15 – 1.43)
Alpha:Touch	9.43	.002	0.11 (0.06)	1.12 (1.03 – 1.21)
Alpha:Light	.06	.8	0.01 (0.04)	1.01 (0.93 – 1.09)
Touch:Light	6.77	.009	0.09 (0.04)	1.09 (1.02 – 1.17)
Alpha:Touch:Light	1.45	.23	-0.05 (0.04)	0.95 (0.88 – 1.03)
Intercept			-1.11(.12)	0.33 (0.26 – 0.41)

Table 2. Summary of the fixed effects of GLMMs of ipsilateral alpha and its influence on reporting of touch. χ^2 statistics derived from likelihood ratio tests, with associated *p*-values. Coefficients and odds ratios reported are from the maximal model as defined above. Confidence intervals for odds ratios were derived using Wald statistics.

Binned alpha power

We analysed both reporting of touch and alpha power as a function of alpha power binned into either quartiles or deciles. We performed these analyses separately for each hemisphere.

Contralateral alpha. For reports of touch, binned power was significant for both quartiles [$F(2.36,73.04) = 3.69$, $p = .02$, $\eta^2_g = .006$] and deciles [$F(6.83,211.8) = 2.77$, $p = .01$, $\eta^2_g = .009$]. There were no significant interactions involving power bin for either quartiles or deciles (all *p*s > .19), so only the main effect of bin is considered here. For quartiles, the linear trend was significant ($t(93) = -2.81$, $p = .006$), with reporting of touch decreasing as power quartile increased; the quadratic fit was not significant ($t(93) = -1.78$, $p = .08$). In post-hoc t-tests, reporting of touch was significantly increased when power was in the 2nd quartile than in the 4th quartile ($p = .014$). No other comparisons were significant. For deciles, both linear ($t(279) = -2.953$, $p = .003$) and quadratic ($t(279) = -2.72$, $p = .007$) trends were

significant, suggesting that reporting of touch declined in an exponential fashion as power bin increased. Post-hoc t-tests found that reporting of touch was significantly higher in the 2nd, 5th, 7th, and 8th decile power bins relative to the 10th power bin (all corrected *p*s < .05). No other comparisons were significant.

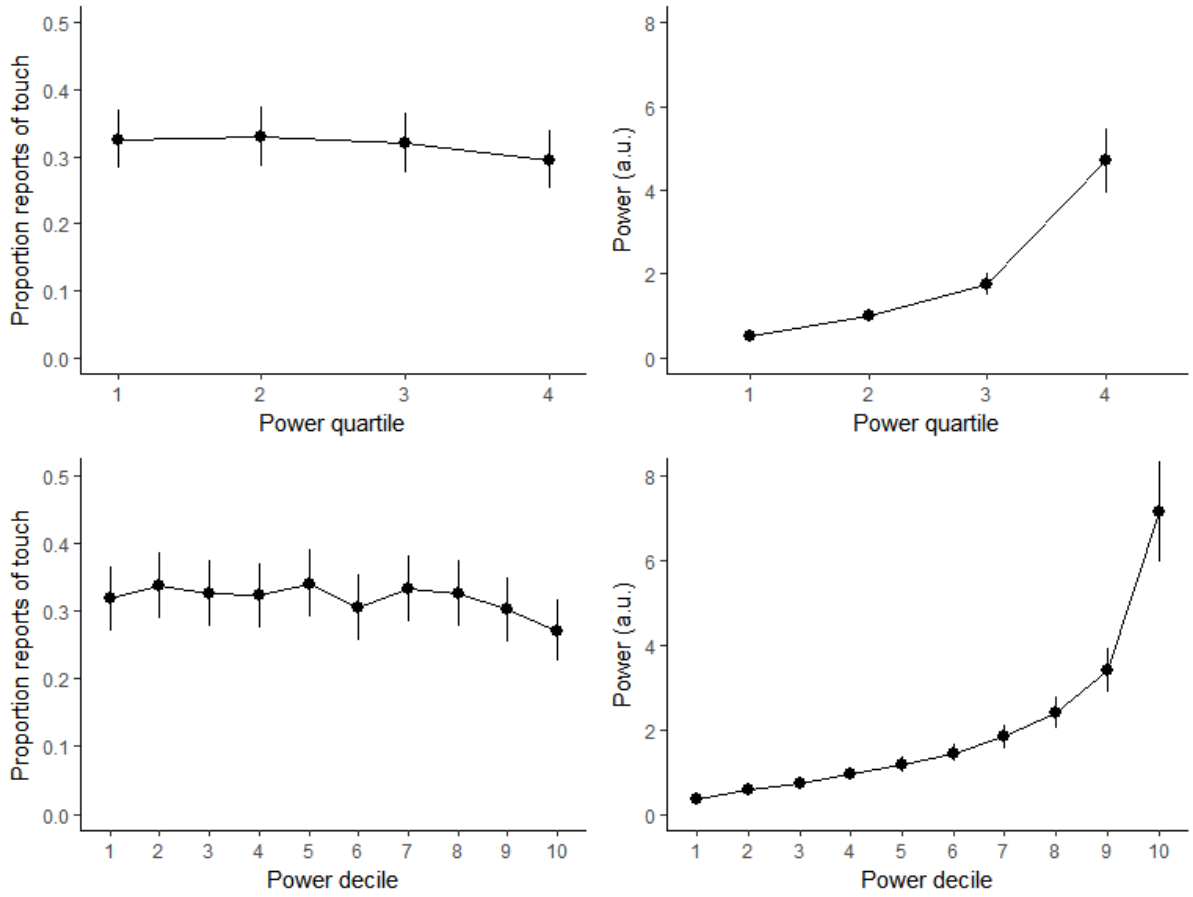

Figure 6. Proportion of touches reported and mean alpha power as a function of binned power for the contralateral hemisphere. Left column shows proportion of trials on which touch was reported in each bin, right column shows mean power per bin. Upper row shows power binned in quartiles, lower row shows power binned in deciles. Errors bars indicate 95% between-subject confidence intervals.

In our analysis of alpha power according to power bin, we found that quartile splits exhibited significant linear ($t(93) = 9.467$, $p < .001$) and quadratic ($t(93) = 3.898$, $p < .001$) trends but no significant cubic trend ($t(93) = 1.371$, $p = .17$). For deciles, the linear ($t(279) =$

14.851), quadratic (t(279) = 7.903) and cubic (t(279) = 4.952) trends were all significant (all *p*s < .001).

Ipsilateral alpha power. For reports of touch, binned ipsilateral power was significant for both quartiles [F(2.92,90.50) = 3.28, p = .03, η^2_g = .005] and deciles [F(6.39,198.18) = 2.31, p = .03, η^2_g = .007]. There were no significant interactions involving power bin for either quartiles or deciles (all *p*s >= .2), so only the main effect of bin is considered further. For quartiles, there was a significant linear trend (t(93) = -3.007, p = .003) but the quadratic (t(93) = -.477, p = .63). and cubic (t(93) = .76, p = .45) trends were not significant. This was also the case for deciles (linear trend: t(279) = -3.119, p = .002; quadratic trend: t(279) = -.67, p = .5; cubic trend: t(279) = 1.477, p = .14).

In our analysis of ipsilateral alpha power according to power bin, we found that quartile splits exhibited significant linear (t(93) = 9.293, p < .001) and quadratic (t(93) = 3.592, p < .001) trends but no significant cubic trend (t(93) = 1.228, p = .22). For deciles, the linear (t(279) = 15.068), quadratic (t(279) = 7.415) and cubic (t(279)=4.460) trends were all significant (all *p*s < .001).

Cluster-based analysis of reported-yes versus reported-no

Our cluster-based permutation analysis of the difference between reported-yes and reported-no trials across the latency range -1s to 0s revealed a significant difference (p < .05) in a single cluster spanning approximately 900 ms before the potential stimulus onset until the time of stimulus onset. The locus of the effect varied across the time-period, beginning initially at contralateral centro-parietal sensors. Note that since the cluster was formed over both time and space, it is possible for seemingly spatially separated clusters to occur in some time periods, since they may have been joined at another time point. Figure 7 shows the

development of pre-stimulus activity binned in periods of 100 ms, highlighting electrodes with significant differences at any time during the specified period.

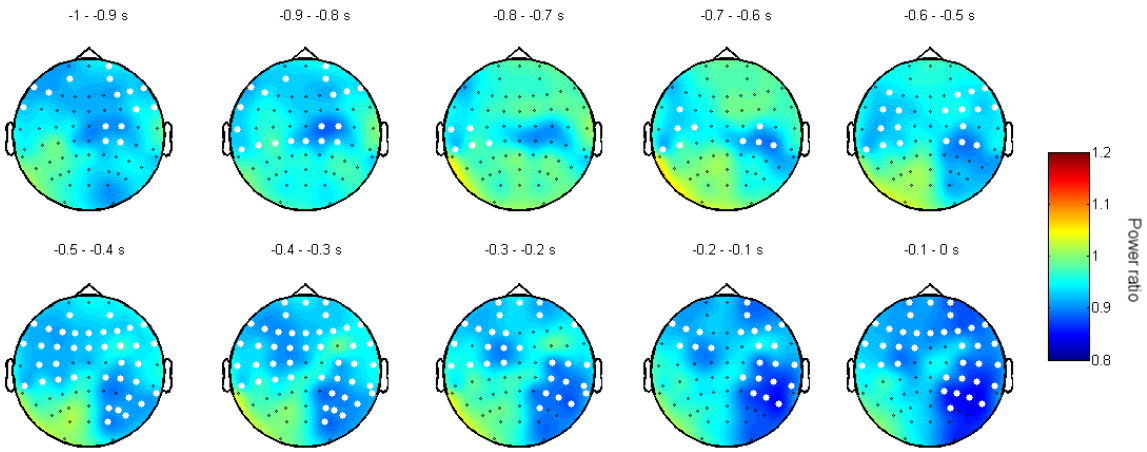

Figure 7. Significant differences in alpha power between the reported-no and reported-yes conditions. Spectral power on reported-yes trials was divided by spectral power on reported-no trials. Red indicates higher power on reported-yes trials, blue higher power on reported-no trials. Electrodes which were members of the significant cluster are highlighted using large white dots; non-significant electrodes are marked with small black dots. Electrodes are highlighted when they were significant at any time throughout the period indicated above each topographical plot.

Notably, electrodes over contralateral centro-parietal cortex, and ipsilateral centro-parietal and temporal regions, partially overlapping our region of interest, exhibit significant higher alpha power from approximately 700-600 ms before potential stimulus onset. Greater left frontal involvement is apparent from approximately 500-300 ms before stimulus onset, before right centro-parietal, posterior parietal, and occipito-parietal electrodes become the dominant region of elevated alpha power in the final 300 ms before stimulus onset. Note that due to temporal smearing from the time-frequency transformation, some of this activity may

reflect early responses to tactile or visual stimuli, particularly in the final 100 ms before stimulus onset.

Discussion

We examined the relationship between somatosensory alpha and the reporting of tactile sensations during the SSDT. We found that pre-stimulus alpha generally followed a negative linear relationship with reporting of touch, with higher alpha associated with a decrease in reports of touch, and lower alpha associated with an increase in reports of touch. The relationship between alpha power and reporting of touch interacted with the actual presence of touch in both hemispheres, exhibiting a weaker but still negative relationship with reporting of touch on trials when a touch was actually present compared to trials when there was no touch. Previous reports of the relationship between changes in somatosensory detection and pre-stimulus alpha power have focused on the hit rate alone, overlooking the concomitant increase in false alarm rate at low levels of alpha. Our results are thus consistent with pre-stimulus alpha over contralateral somatosensory cortex bringing about shifts in response criterion: low alpha power increases both true and false reports of touch, whereas high alpha power decreases both true and false reports of touch. We found bigger effects on tactile-absent trials, suggesting that alpha may have a stronger role in determining responses in the absence of touch. We also found no evidence that pre-stimulus alpha modulated the effect of the light on reporting of touch, or that the relationship between pre-stimulus alpha on reporting touch was influenced by the presence of light.

We found a negative linear relationship between alpha power and reporting of touch, in keeping with some previous studies (Jones et al., 2010; van Ede et al., 2012). Lower alpha power over contralateral somatosensory cortex was associated with an increase in both correct and false reports of touch. Reports of touch overall declined with increasing alpha

power, albeit at a faster rate for false alarms. Thus, the relationship appears to index a shift in response criterion rather than in tactile sensitivity, similar to recent reports on the relationship between visual alpha and performance on a visual task (Limbach & Corballis, 2016; Sherman et al., 2016). Physiologically, a linear relationship between alpha power and performance might reflect the relationship between alpha and cortical excitability (Jensen & Mazaheri, 2010; Klimesch et al., 2007; Ploner, Gross, Timmermann, Pollok, & Schnitzler, 2006). Under this account, low alpha power indicates high excitability, while high alpha indicates low excitability. Our finding of increases in both correct and false reports of touch is consistent with this hypothesis. In a high excitability state, participants were more likely to report touch than in a low-excitability state. Cognitively, this might also reflect fluctuations in attentional state, which may be instantiated through changes in excitability.

For our generalized linear mixed effects analysis, we averaged power across a time window from -600ms to -200ms before the potential onset of a tactile stimulus at two specific clusters of electrodes. It is thus possible that we did not capture all of the relevant spatio-temporal variation in the relationship between alpha oscillations and tactile detection. In effect, we treat alpha power here as a summary of the overall state in the specified time-window. Nevertheless, momentary variations in excitability as indexed by the phase of oscillations are likely to also be important (e.g. Ai & Ro, 2014; Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008; Sherman et al., 2016) and may have other relationships with performance than the overall state as indexed here. Future investigations which directly manipulate ongoing oscillations through methods such as transcranial alternating current stimulation (Helfrich et al., 2014; Herrmann, Murray, Ionta, Hutt, & Lefebvre, 2016; Vosskuhl, Huster, & Herrmann, 2016) would help to answer these questions more directly.

Our cluster-based analysis suggests that the specific electrodes on which significant effects can be observed shifts across the majority of the pre-stimulus window, but also

overlap (at least partially) with our regions of interest. Notably, our a priori contralateral cluster showed significantly higher alpha power on reported-no than reported-yes trials from around -700ms until the onset of the stimulus. Ipsilateral regions also showed significant higher alpha power from around -900ms until -300ms, which spread in a more diffuse fashion to temporal and frontal sensors than our a priori ipsilateral cluster. These results are thus consistent with the overall finding of our regression analysis, which would predict that alpha power should be higher on reported-no than reported-yes trials, and those of Limbach and Corballis (2016), who found that pre-stimulus alpha power was lower for both hits and false alarms than for misses and correct rejections.

We found little evidence for a role of pre-stimulus alpha power on the effect of reporting touch in the presence of a light, either in terms of its effects when light was presented alone or when the light was presented simultaneous with the touch. Increases in reporting of touch attributable to the light may be related to post-stimulus phase resets of ongoing oscillations. Stimuli in one sensory modality have been shown to influence ongoing activity cross-modally, e.g. phase resets in visual cortex following an auditory stimulus (e.g. Naue et al., 2011; Romei, Gross, & Thut, 2012). Figure 3A shows that this may be possible here, given that changes in somatosensory alpha occurred after the light, even when no touch was present. In addition, the lack of pre-stimulus effects involving the light suggests our findings are unlikely to reflect top-down modulations of alpha in order to ignore the light.

A number of studies have reported quadratic rather than linear relationships between alpha power and performance on several tactile tasks (Ai & Ro, 2014; Linkenkaer-Hansen et al., 2004; Weisz et al., 2014; Zhang & Ding, 2010). Typically, in these studies hit rates are highest at an intermediate level of alpha power. These findings are interpreted as indicating alpha functions as an intrinsic source of noise, modulating hit rates through stochastic resonance. Stochastic resonance is a phenomenon in which the addition of noise to a non-

linear system boosts or improves transmission or detection of a signal (McDonnell & Abbott, 2009). A parabolic relationship between performance and noise is a key characteristic of stochastic resonance. However, these reports in the somatosensory domain have not taken the possibility of changes in false alarm rate with changes in alpha power into account, and thus may have underestimated the downside of variations of alpha power (Ai & Ro, 2014; Linkenkaer-Hansen et al., 2004; Weisz et al., 2014; Zhang & Ding, 2010).

Some of the variation in results may be due to differences in analysis methods. We modelled power as a continuous variable, rather than binning trials into groups from low to high power as has been typical practice (Ai & Ro, 2014; Linkenkaer-Hansen et al., 2004; Weisz et al., 2014; Zhang & Ding, 2010). As we report here, the shape of the detected relationship between alpha power and performance may differ according to the number of bins. We found a significant linear trend and a borderline non-significant quadratic trend when a quartile split was used, while a decile split led to significant linear, quadratic, cubic, and quartic terms. As we also report, quartile and decile splits led to a quadratic relationship between alpha power and bin, with the 4^{th} quartile and 10^{th} decile respectively showing markedly higher mean alpha power than the preceding bins, and higher variability around that mean. The distribution of alpha power shows a strong positive skew with a long tail, similar to a log-normal distribution. Whatever the underlying relationship between alpha power and performance, the non-linearity introduced by binning obscures it. Since quartile (Weisz et al., 2014), quintile (Limbach & Corballis, 2016), and decile (Zhang & Ding, 2010) splits have been used previously in the literature, this may account for some of the variability in the patterns of results found by different research groups. We thus recommend that researchers choose analytical methods that do not require binning wherever possible.

Additionally, both contralateral and ipsilateral levels of somatosensory alpha may be important (Haegens, Luther, & Jensen, 2012; van Ede, de Lange, & Maris, 2013). We found a

similar negative relationship between alpha and reporting of touch over ipsilateral somatosensory cortex on touch absent trials as we found over contralateral cortex. Alpha over sensory regions other than the primary region associated with a task may play a key role in suppressing irrelevant information – the gating-by-inhibition hypothesis – as seen in a number of studies of spatial attention (Gray, Frey, Wilson, & Foxe, 2015; Haegens et al., 2011, 2011; Jensen & Mazaheri, 2010). Thus, when attending to the right hand, alpha power increases over right, ipsilateral somatosensory cortices and decreases over left, contralateral somatosensory cortices. This relationship is typically present when a stimulus is presented to one hand and a distractor presented to another, although it has been observed even without distractors (Haegens et al., 2012). Here, no strong decrease in ipsilateral power was observed. This may be due to the absence of distracting stimuli presented to the right hand. Thus, there was no need to actively suppress sensory input from the right hand. Nevertheless, there was an overall decrease in reporting of tactile stimuli with increasing levels of alpha in both contralateral and ipsilateral somatosensory regions, suggesting that in both regions increased alpha power suppressed sensory responses.

In conclusion, we found that participants were more likely to report that they felt a touch when contralateral pre-stimulus alpha power was relatively low, and less likely to report that they felt a touch when contralateral pre-stimulus alpha power was relatively high. For the first time in the somatosensory domain, we have shown that this relationship was even stronger for false reports than for true reports. Thus, our results suggest that alpha power indexes shifts in response criterion rather than sensitivity alone, since increases in hit rate were also accompanied by increases in false alarm rate. Accounts of the role of pre-stimulus oscillatory activity in predicting perception should explain its effects on both veridical perception and on false misperceptions.

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